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# Amitrole Absorption by Bean (*Phaseolus vulgaris* L. cv 'Red Kidney') Roots[1]

## MECHANISM OF ABSORPTION

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### ABSTRACT

**The mechanism of transport of the herbicide 3-amino-1,2,4-triazole (amitrole) into *Phaseolus vulgaris* roots appears to be passive, as judged by the effect of temperature ($Q_{10}$ = 1.3 between 15 and 25°C) and the lack of sensitivity to metabolic inhibition afforded by 2,4-dinitrophenol and $NaN_3$. Amitrole absorption is a linear function of external concentration over several orders of magnitude and, thus, is not facilitated by a carrier mechanism. The absorption of amitrole is sensitive to external pH, being stimulated under acid conditions. This stimulation of amitrole absorption is seen at low (≤1 millimolar) amitrole concentrations, but not at high (50 millimolar) amitrole levels. While the apparent octanol-water partition coefficient varies with the pH of the aqueous phase, there is no clear correspondence between absorption and the apparent partition coefficient. Roots do not accumulate amitrole above concentration equilibrium; however, at a time when the net amitrole content of the root tissue begins to saturate, amitrole can be detected in the xylem stream. On a fresh-weight basis, amitrole absorption by roots is equal to that accomplished by trifoliate-leaf tissue. An estimate of the permeability coefficient (according to the analysis of Tyree et al. 1979 Plant Physiol 63: 367–374) suggests that amitrole possesses near-optimal permeability for an ambimobile solute, on the order of 2.12 (± 0.47) × $10^{-9}$ meters per second.**

The mechanism(s) by which polar solutes negotiate the barrier of cell wall and plasmalemma are topics of continued interest to plant physiologists. In particular, knowledge of the means by which xenobiotics enter the symplast is of both theoretical and practical concern. The water-soluble herbicide, 3-amino-1,2,4-triazole (amitrole), is a compound which shows extensive xylem and phloem mobility in a variety of plant species and is relatively nonselective in its phytotoxicity. Amitrole has been proposed to exert its herbicidal activity by several modes of action, including interference in Chl biosynthesis and disruption of histidine metabolism (see 1 and 2). Regardless of the actual mechanism of action, amitrole must clearly penetrate one or more membrane systems in order to exert its effect. An understanding of the factors which contribute to its penetrability may therefore allow one to increase efficacy while limiting the amount of material released into the environment. This study was conducted with the aim of elucidating the mechanism by which amitrole is absorbed.

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### MATERIALS AND METHODS

**Plant Material.** Plants for root uptake and permeability studies were prepared as follows: seeds of *Phaseolus vulgaris* L. cv 'Red Kidney' were surface sterilized in 1% NaOCl, rinsed in running tap water for 18 h, and sown onto stainless steel screens suspended over black Plexiglas boxes containing 0.25× Johnson's modified Hoagland solution (10). These plants were grown in a dark chamber at 25°C for a period of 5 to 8 d; the growth medium was changed on either day 2 or 3.

**Root Absorption Studies.** Root uptake studies were performed in Plexiglas chambers of two or more compartments placed in a thermostated bath. In most experiments, roots were sealed through holes in compartment dividers with silicone vacuum grease (Dow Corning Corporation). Thus, the distal 0.5 cm (compartment A), the more proximal 2.5 cm (compartment B), and the remaining portion of the primary root up to the region of emergence from the seed (compartment C) were effectively isolated from each other. Treatment with radioactive herbicide could be accomplished in any of these three compartments, and uptake by and transfer from the treated segments determined by excising the treated and untreated portions and sampling the solution contained in the other compartments. In most cases, [$^{14}$C]amitrole was added to compartment B; over a 30-min uptake period, no counts above background were found in either the tissue or solution in compartments A or C. Mixing and aeration in the compartment containing the label was accomplished by a stream of humidified air delivered by a polyethylene tube. For experiments involving uptake by roots and transfer of the label to the xylem (Fig. 4), the proximal 0.2 cm of root protruded into compartment A; the divider between sections B and C was removed.

Radioactivity was assayed by liquid scintillation counting in a mixture of toluene: Triton X-100 (2:1, v/v) containing 4 g/L Omnifluor (New England Nuclear) on a Beckman LS 8000 LS-counter at efficiencies ranging from 85 to 96%. Results are expressed as quantity of amitrole absorbed per unit fresh weight per unit time (mean ± SE).

**Estimation of Permeability Coefficient.** Seedlings were dark-grown under the conditions described above. When the roots of the seedlings reached a length of at least 3 cm (usually 6–8 d after planting), the root apex was excised. The remainder of the primary root below the lateral root zone was cut into segments approximately 3 cm in length. Segments were placed in 0.25× Johnson's modified Hoagland solution until ready for use.

Approximately 65 root segments were placed into each uptake vessel (7 ml disposable polyethylene scintillation vial). Segments were packed carefully to avoid tissue damage. To each vial, 5.0 ml of pretreatment solution was added and the segments were continuously aerated with humidified air for 15 min. At the end of this period, the pretreatment solution was removed, 5.0 ml uptake

solution (10 μM in amitrole) was added, and vials were sampled immediately. Two samples of 25 μl each were taken from each vial at subsequent intervals of 2 to 20 min up to a total of 180 min. The radioactivity in each sample was measured as described above. From a graph of the log of the disappearance of labeled herbicide (corrected for the differences in volume between bathing solution and symplast) *versus* time, an apparent half-time for this disappearance can be calculated (see equation in Ref. 19). Using this value for the half-time, an estimate of the permeability, $P^*$, can be found as developed by Tyree *et al.* (19) where

$$P^* = \frac{V_1}{A}\frac{V_2}{V_1 + V_2}\frac{\ln 2}{t_{1/2}}$$

In this equation, $P^*$ represents the permeability coefficient (in m $s^{-1}$); $V_1$, symplastic volume; $V_2$, volume of the external solution; $A$, cumulative cellular surface area; $t_{1/2}$, the half-time for disappearance of chemical from external solution (see above); and ln 2, the natural logarithm of 2.

**Measurement of Cell Dimensions.** Beans were planted and grown as described above. Approximately 6 d after planting, roots were sectioned by razor blade into radial and longitudinal sections. Sections were stained with basic fuchsin-toluidine blue and measured using a calibrated ocular micrometer at a magnification of 288×. Cortical cells were found to have an average diameter of 45 μm and an average length of 97 μm.

**Leaf Disc Absorption Studies.** The youngest, fully expanded trifoliate leaves of greenhouse-grown *P. vulgaris* L. cv 'Red Kidney' plants were used for uptake studies. To disrupt the cuticle, the abaxial surface of the leaf was brushed lightly with dry Carborundum (Fisher Chemical Company) and a soft-bristled paintbrush for up to 50 strokes. Excess abrasive was shaken off the leaf, and discs 0.38 $cm^2$ in area where cut with a sharpened cork borer. The discs were placed abraded-surface down in preincubation solution, until all discs were collected. These were transferred sequentially to uptake solutions (30 min) and then to rinse solutions (10 min). The treated discs were placed into scintillation vials, where they were cleared by additions of 7% $HClO_4$ (0.2 ml), 30% $H_2O_2$ (0.2 ml), and methyl cellosolve (two drops) (8). Scintillation fluid (Filter-Solv; Beckman Instruments) was added and radioactivity determined as described above.

**Identity of Transported Molecule.** To confirm the presence of the $^{14}C$ label in authentic amitrole, thin-layer chromatograms were performed on material extracted from bean roots. To approximately 1.0 g of root material (allowed to absorb amitrole for the time period indicated), 5 ml of 100% ethanol was added and the mixture homogenized in a mortar and pestle. The slurry was filtered and the clear extract evaporated to dryness under a stream of $N_2$. The dried material was resuspended in 1.0 ml of 10% *n*-propanol, and the volume reduced under $N_2$ to approximately one-half. This mixture was spotted onto 5 × 20 cm cellulose thin-layer plates and developed in a solvent system of *n*-propanol:$NH_4OH$:$H_2O$ (3:1:1, v/v/v) (17). Unlabeled, authentic amitrole was spotted onto lanes at the margins of each plate. Following development, the center of the plates (containing the radioactivity) were masked, and the plates were sprayed with 0.2% ninhydrin in ethanol (Sigma Chemical Company). The zone corresponding to authentic amitrole was identified and the plate divided into 0.75-cm bands perpendicular to the direction of solvent movement. These zones were scraped from the plate and placed into scintillation vials, to which 0.4 ml of methyl cellosolve was added, followed by 0.65 ml absolute ethanol and 6 ml scintillation fluid. After counting, the relative amount of radioactivity remaining as amitrole was calculated.

**Partition Coefficient.** Labeled amitrole was added to 22 ml scintillation vials containing equal volumes of buffer and 2-octanol. The vials were placed on a wrist arm shaker for 6 h and the aqueous and organic phases sampled after clear separation of phases occurred. After correcting for counting efficiency, the partition coefficient was calculated by dividing the number of dpm in the organic phase by those in the aqueous phase.

**Reagents and Solutions.** Chemicals used in this study are reagent grade from commercial sources; amitrole (analytical grade) was obtained from Union Carbide and from Sigma Chemical Company. Labeled amitrole was obtained from Union Carbide (3,5-[$^{14}C$]) and New England Nuclear (5-[$^{14}C$]) at initial specific activities of 4.02 and 5.43 mCi/mmol, respectively. No attempt was made to purify the radioactive herbicide further, since TLC in the solvent system described above showed that >97% of the label cochromatographed with analytical grade material.

Pretreatment solutions for root absorption and permeability coefficient studies contained (in mM): 10, buffer (Mes for pH 4, 5, 6; MOPS,[3] 7; Tes, 8; TAPS, 9; CAPS, 10); 0.1, $Ca^{2+}$; 0.5, $K^+$; 1.6, $Cl^-$; 0.1, $Mg^{2+}$; 1.0, $Na^+$. Uptake solution for root absorption was as above and contained amitrole at the concentration and specific activity noted in the figure legends. For permeability coefficient studies, the uptake solution was supplemented with 10 mM $CaCl_2$. Rinse solution (to remove free space label) was identical to uptake solution, but minus labeled amitrole and supplemented with 5 mM $CaCl_2$.

## RESULTS

Initial experiments showed that, over the course of at least 30 min, amitrole absorption by detached roots shows a biphasic pattern with respect to time (Fig. 1, upper curve). If the roots were subjected to a 10-min rinse in rinse solution (pretreatment solution supplemented with 5 mM $CaCl_2$ and 1 mM amitrole) immediately following the uptake period, this biphasic response was replaced by a linear dependence (Fig. 1, lower curve). There were no qualitative or quantitative differences in these results presented above when the experiments were performed on attached roots (data not shown).

Using this 30-min absorption period, followed by a 10-min

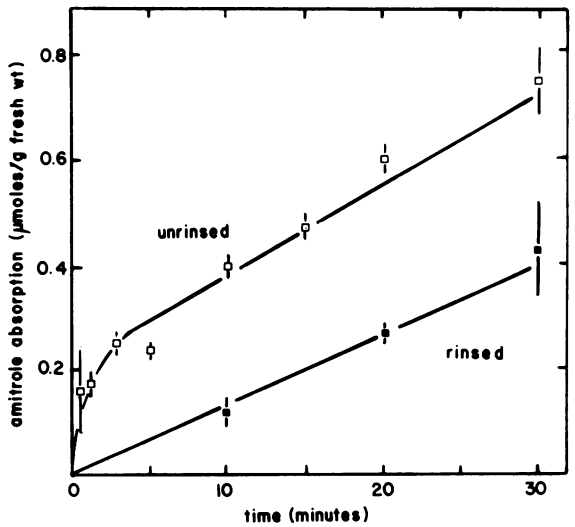


FIG. 1. Amitrole absorption by *Phaseolus* roots as a function of time. Amitrole absorption in detached bean roots was measured as described in "Materials and Methods." Amitrole concentration was 1.0 mM; 0.01 μCi/μmol; external pH, 6.0. At the end of the 30-min absorption period, roots were or were not treated for 10 min in rinse solution. Data are expressed as mean ± SE for two experiments.

[3] Abbreviations: MOPS, 3-(4-morpholino)propanesulfonic acid; CAPS, 3-(cyclohexylamino)propanesulfonic acid; DNP, 2,4-dinitrophenol; TAPS, tris(Hydroxymethyl)methylaminopropanesulfonic acid.

rinse, the concentration and temperature dependence and inhibitor sensitivity of amitrole uptake was investigated. Over concentration ranges from 0.5 μM to 100 mM, uptake remained linear (Fig. 2, A–C). In addition, treatment with the metabolic inhibitor, $NaN_3$, and protonophore, DNP, did not reduce uptake significantly (Table I). The effect of temperature is shown in Figure 3, where uptake was stimulated by increasing temperature up to 33°C; above 33°C, uptake declined. Between 15 and 25°C, the calculated $Q_{10}$ value is 1.3, indicating an activation energy for amitrole absorption of about 5 kcal/mol.

With longer absorption periods, the total amount of amitrole taken up by the root tissue began to saturate (Fig. 4). At 3 h, the increase in $^{14}C$ material in the tissue was no longer linear with time, and label also began to be detected in the xylem fluid. By 24 h, amitrole content approached 1.0 μmol/g root, and about 0.4 μmol label/g root tissue had been transferred to the compartment representing the xylem system. By using frozen-thawed root segments in place of the detached roots, it was demonstrated that less than 15% of the total amitrole transferred at 24 h could be accounted for by diffusion through the apoplast. In both the xylem

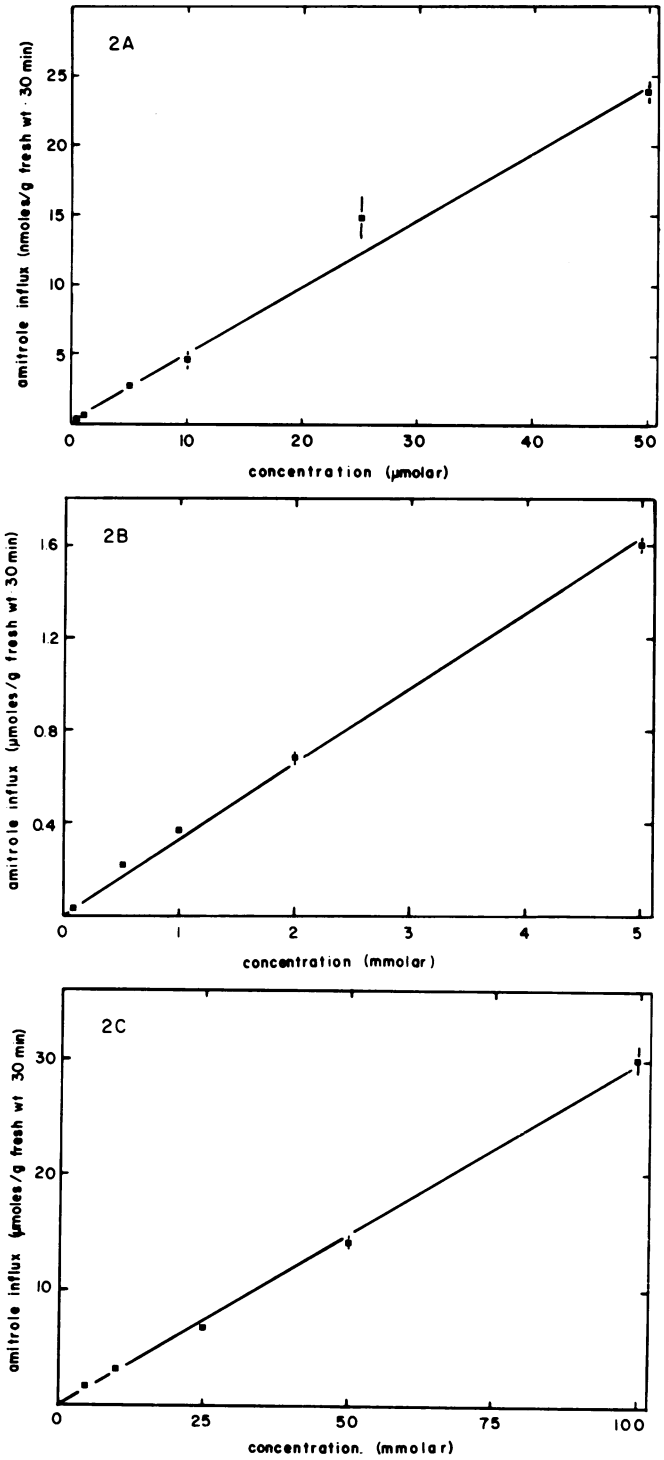


FIG. 2. Amitrole absorption as a function of amitrole concentration. Amitrole absorption in detached bean roots was measured as described. Data points represent mean ± SEM for a minimum of six determinations (two experiments) with seven detached roots per determination. A, Amitrole absorption between 0.5 and 50 μM [amitrole]; B, amitrole absorption between 50 μM and 5 mM [amitrole]; C, amitrole absorption over the concentration range 5 to 100 μM [amitrole]. Specific activities of the amitrole solutions ranged from 0.005 to 2.5 μCi/μmol.

Table I. *Effect of Metabolic Inhibitors on Amitrole Absorption by Phaseolus Roots*

Amitrole absorption was measured over a 30-min period at a concentration of 1.0 mM and specific activity of 0.01 μCi/μmol, as described. External pH was 6.0. Results are expressed as the mean ± SE ($n = 6$ for control and DNP determination [two experiments]; $n = 3$ for $NaN_3$ [one experiment]).

| Treatment[a] | Absorption Rate of Amitrole |
|---|---|
| | *μmol/g fresh wt·30 min* |
| Control | 0.43 ± 0.03 |
| DNP (0.1 mM) | 0.40 ± 0.06 |
| $NaN_3$ (1.0 mM) | 0.39 ± 0.06 |

[a] Inhibitor treatment commenced 30 min before addition of labeled amitrole.

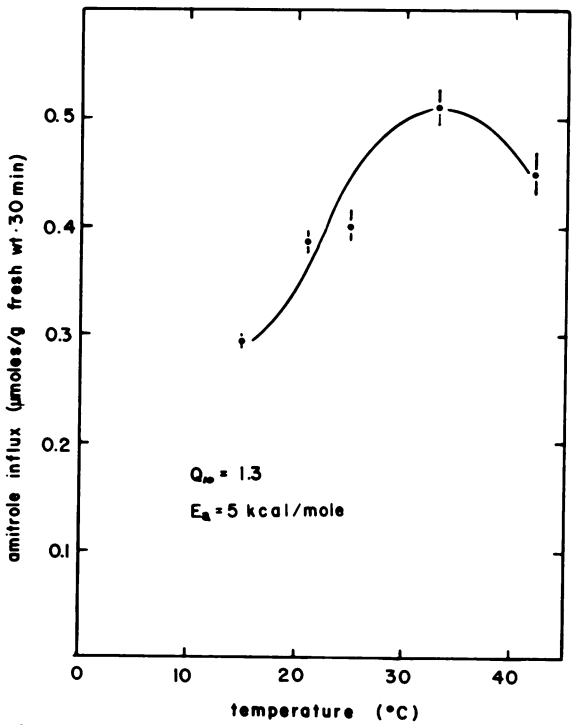


FIG. 3. Effect of temperature on amitrole absorption by bean roots. Amitrole absorption was measured by detached bean roots as described. Conditions are as described in Figure 1. The initial incubation was lengthened to 30 min to allow thermal equilibration. Results are expressed as mean ± SE for three experiments.

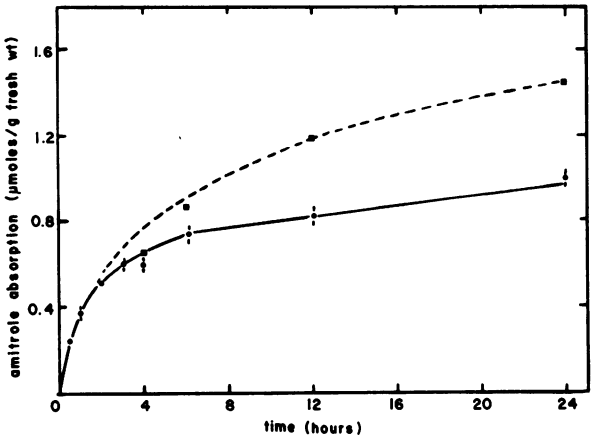


FIG. 4. Amitrole absorption and transfer to xylem by detached bean roots. Amitrole absorption was measured as described. Amitrole concentration was 1.0 mM; 0.01 μCi/μmol; external pH, 6.0. (●——●), Amount of amitrol detected in the root tissue at the indicated times. Data is expressed as mean ± SE for two experiments, for a total of six determinations. (■- - -■), Mean amount of amitrole detected in the tissue plus the amount transferred to the xylem compartment.

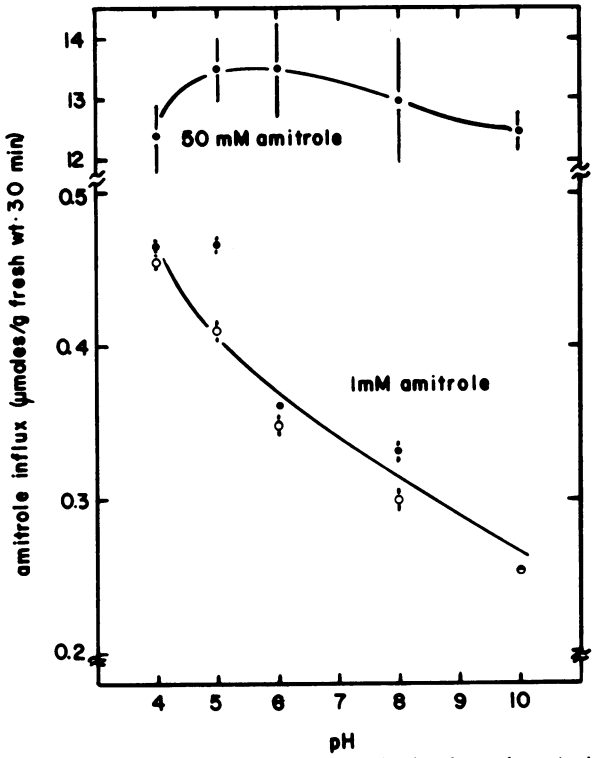


FIG. 5. Influence of external pH on amitrole absorption. Amitrole uptake measured as described in "Materials and Methods" over a 30-min period, with solutions buffered with 10 mM zwitterionic buffers (●) or sodium phosphate (○). External amitrole concentration was 1.0 mM. Results are expressed as mean ± SE for three experiments (three samples of seven roots per experiment) in each buffer system.

fluid and in the root tissue, the label remains as amitrole, as judged by cellulose TLC in the solvent system listed in "Materials and Methods." Greater than 90% of the total radioactivity in the xylem fluid sampled at 4, 12, and 24 h cochromatographs with authentic amitrole. Extracts of roots exposed for 12 and 24 h to 1.0 mM amitrole had 91 ± 4% and 87 ± 4% of the label, respectively, as amitrole.

The dramatic effect of external pH on amitrole absorption from a 1.0 mM external solution by bean roots is depicted in Figure 5. This effect is independent of the buffer system used (Na-phosphate or zwitterionic). However, acid stimulation of absorption is eliminated by increasing the amitrole concentration to 50 mM (Fig. 5). At concentrations less than 1.0 mM, the pH effect is conserved (data not shown).

The apparent octanol-water partition coefficient shows variation with pH of the aqueous phase (Fig. 6). Between pH 5 and 10, there is no large change in partition coefficient. Below pH 5 and above pH 10, amitrole becomes increasingly water soluble.

The half-time for disappearance of labeled amitrole from a solution surrounding the roots was 40 ± 5 min (mean ± SE) for five experiments. For the (cylindrical) cortical cells, the surface area-to-volume ratio was calculated to be $9.13 \times 10^{-6}$ $m^{-1}$; apparent symplasmic volume ($V_1$) was estimated from the fresh weight-dry weight difference of each sample. Using the relationship to estimate the permeability, $P^*$, as described in "Materials and Methods," it was found that $P^* = 2.12\ (\pm 0.47) \times 10^{-9}$ m $s^{-1}$ (mean ± SE) for five experiments.

The relationship between foliar *versus* root-mediated absorption was investigated by comparing amitrole uptake in abraded leaf discs and detached roots (Table II). Over a 30-min absorption period, root tissue absorbed an equal amount of amitrole as did leaf discs, when compared on fresh-weight basis.

## DISCUSSION

The pattern of amitrole absorption as a function of time (Fig. 1) showed a biphasic response over the period examined, consisting of initial rapid movement into the tissue which was completed

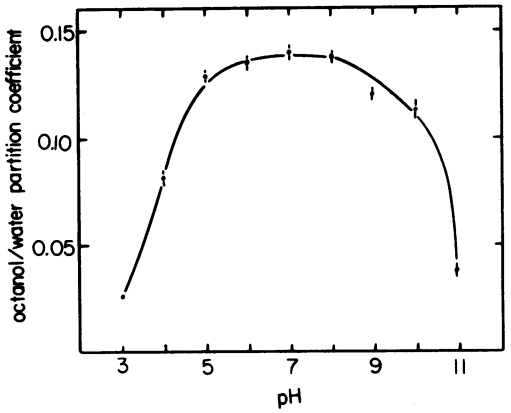


FIG. 6. Partition coefficient of amitrole as a function of pH of the aqueous phase. The partition coefficient (octanol-water) was determined as described in "Materials and Methods." Data represents pooled results in which the aqueous phase is buffered with either zwitterionic or sodium phosphate buffer (10 mM). Specific activity of the amitrole solution was 0.01 μCi/μmol. A minimum of three experiments (ten samples per experiment) were performed with sodium phosphate buffer; one experiment at each pH was performed with the zwitterionic buffers. Data are expressed as the mean ± SE.

Table II. *Comparison of Amitrole Absorption by Phaseolus Root and Leaf Tissue*

Amitrole absorption was measured as described, at an external pH of 6.0, amitrole concentration of 1.0 mM, and specific activity of 0.01 μCi/μmol. Data are expressed as mean ± SE. Root data are taken from Figure 2; leaf absorption data are based on two experiments (10 determinations per experiment).

| Absorbing Organ | Absorption Rates |
|---|---|
| | *μmol/g fresh wt·30 min* |
| Roots | 0.37 ± 0.01 |
| Leaf discs | 0.33 ± 0.02 |

within 5 to 10 min, followed by a steady but slower absorption phase. This pattern has been observed for absorption for a variety of solutes by various tissues; it is interpreted as an initial movement into the free space of the tissue followed by subsequent transport into the symplast (3). This is substantiated further by the fact that a rinse period of 10 min in unlabeled amitrole solution effectively eliminated the initial rapid phase (Fig. 1), but not the second slower phase. The rinse time needed to eliminate the contribution of the free space component, as determined empirically here, was also in close agreement to the time necessary to allow diffusion out of the free space, as determined by efflux analysis on preloaded detached roots (data not shown). Thus, a 30-min absorption period/10-min rinse period will allow a characterization of transport at the level of the plasmalemma and minimize the contribution of the label contained in the free space.

Amitrole absorption by root tissue of *P. vulgaris* appeared to occur passively and in a non-carrier-mediated manner, as judged by concentration (Fig. 2, A–C) and temperature (Fig. 3) dependence, as well as by the insensitivity of this process to metabolic inhibitors (Table I), over a period when amitrole absorption was linear with respect to time (Fig. 1). In this regard, the passive absorption of amitrole is similar to that seen for many xenobiotic compounds in plants, including, for example, monuron (5), glyphosate (9), and oxamyl (12). A report that documents the mechanism of uptake of amitrole by suspension-cultured tobacco cells and protoplasts reaches similar conclusions as to the passive non-carrier-mediated uptake of this molecule (16).

Amitrole accumulation in root tissue (Fig. 4) began to level off between 4 and 6 h; by 24 h, the concentration in the tissue reached approximately 0.9 μmol/g fresh weight with an external amitrole concentration of 1.0 mM. Measurement of tissue dry and fresh weights showed that about 90% of the root weight was water; the remaining 10% represented structural components of the cells, the majority of which was cell walls. Assuming the relationship of 1.0 g fresh weight equals 0.9 ml water, the equilibrium concentration ratio of internal to external amitrole was unity, the ratio expected for nonionized or electrically neutral solute absorbed passively. That amitrole exists in the electrically neutral form is also consistent with results from the determination of the apparent partition coefficient. Below pH 5 and above pH 8, the apparent partition coefficient indicates that amitrole becomes more water-soluble, expected for a molecule existing in an ionized state. Between pH 5 and 8, the molecule shows the highest value for partitioning into the nonaqueous phase; this represent the zwitterionic or neutral form of the molecule, expected to be the major form of the molecule existing in the cytoplasm, vacuole, and external solution.

Amitrole absorbed by the roots could be transferred to the xylem (Fig. 4; difference between upper and lower curves). TLC of extracts of root tissue and of the xylem exudate showed that the material absorbed and transferred was authentic amitrole. This is unlike the breakdown of amitrole by bean leaves (17), where only about 30% of the initial [$^{14}$C]amitrole applied remained unmetabolized after 24 h. Thus, the amitrole molecule could be absorbed by the roots and transferred unaltered, in appreciable quantities, to the xylem. It is also of interest to note that this condition of no pressure gradient across the root cell/xylem element interface appproximates the situation found in guttating systems. The mass transfer of xenobiotics under conditions of transpiration demand (and hence, a large pressure differential between xylem element and cortical apoplast) remains to be examined in future studies.

As has been found previously for picloram (15, 18) and glyphosate (Fernandez and Bayer, personal communication), absorption of amitrole is stimulated almost 2-fold when the pH of 1.0 mM amitrole solution surrounding bean roots is decreased from pH 10 to 4 (Fig. 5). The partition coefficient for amitrole, a measure of the lipid solubility and charge characteristics, varied with pH (Fig. 6); however, no clear correlation can be seen between this relationship and pH-dependent amitrole uptake. If amitrole behaved like the herbicide, 2,4-D, or other weak acids in its absorption, then uptake should be greatest at the pH where lipid solubility is maximal, *i.e.* below the pK of the carboxyl group (reviewed in 13). In fact, comparison of Figures 1 and 2 demonstrates that amitrole absorption shows no clear dependence on lipid solubility, as estimated by the apparent partition coefficient. Thus, a weak-acid mechanism, postulated to explain the effects of pH on cellular absorption and phloem transport (4), does not seem to operate in the instance of amitrole absorption. One possibility for the effect of pH on absorption may be the influence of proton concentration on the binding of amitrole to some extracellular or cellular structure(s). Labeled amitrole is associated with segments of frozen-thawed, acid-washed *Phaseolus* roots and this association can be reversed by low pH or increasing concentrations of mono- or divalent cations (Lichtner, unpublished results). Amitrole binding to soil organic matter is pH sensitive (11), and amitrole behaves as a cation in its exchange properties on montmorillonite clay surfaces (14); electrostatic interactions of the amitrole molecule are not without precedent. Singer and McDaniel (16) have determined that a significant portion of amitrole is bound to cellular material (primarily cell walls) pelleted by a 1-min centrifugation at 1,610*g*. The proportion bound increased at increased amitrole concentrations. Likewise, Donalley and Reis (6) have suggested that a portion of the amitrole absorbed by *Agropyron repens* is unavailable for translocation and bound at the site of application; addition of ammonium salts frees some of this bound material for subsequent translocation out of the leaf.

Previous workers (16) investigating the effect of pH on amitrole uptake have not observed such a dependence, although only one amitrole concentration was used, and this study clearly shows the pH response to be concentration dependent. Additional differences between these studies are that Singer and McDaniel (16) utilized suspension-cultured cells to examine pH effects while whole root tissue was employed in this investigation, as well as an obvious difference in the plant species used.

Amitrole absorption by roots was equal (over a 30-min period) to that by leaf discs of trifoliate leaves, at identical external pH and amitrole concentration (Table II). Since abraded leaf material was used, amitrole uptake was no longer limited by a cuticular barrier on the leaf surface; abrasion of the cuticle greatly increases the conductance of the cuticle to polar solutes (7). The schedule of abrasion used permitted maximal uptake with regard to nonabraded controls; there is approximately a 2-fold enhancement of uptake by abraded discs over nonabraded controls. The fact that uptake by root and leaf material was of similar magnitude suggests, but does not conclusively demonstrate, that a similar mechanism of uptake may operate in amitrole absorption by leaf cells.

The estimate of the permeability coefficient for amitrole absorption lies close to the theoretical optimum for effective transport of xenobiotics in the phloem under certain specified conditions, as calculated by Tyree *et al.* (19). Inasmuch as their calculations are based on a linearized, or simplified source/sink translocation pathway of defined dimension and translocation velocity, it is difficult to predict optimum permeabilities for different species or from different size plants of the same species. Application of this theory also assumes that the permeability barrier in the phloem to passively absorbed molecules is similar to that of root cells. Even with these caveats taken into account, my determination of the permeability of amitrole in root cells was close to the optimum permeability predicted for ambimobile xenobiotics (19). This was a slightly lower value than that measured for glyphosphate in sugar beets (*Beta vulgaris* L.) (9); however, this value for glyphosate was within the range of optimum permeabilities predicted for sugar beets under the conditions of their assay. Both amitrole and glyphosate show excellent mobility within a variety

of plants with accumulation in active sinks; such a pattern suggests that these molecules should show, a priori, near-optimum membrane permeability characteristics. Gougler and Geiger (9) have shown that glyphosate absorption was most adequately described by the intermediate permeability theory (12), rather than the weak-acid mechanism (4). The results presented in this paper suggest that amitrole absorption may also be described according to the former theory.

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